The arid land invasive weed *Nicotiana glauca* R. Graham (Solanaceae): Population and soil seed bank dynamics, seed germination patterns and seedling response to flood and drought

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1. Introduction

Nicotiana glauca, a fast growing shrub or small tree native to South America, belongs to the family Solanaceae (Mizrachi et al., 2000). It branches profusely, and can grow vigorously to a height of 3 m, particularly after substantial rainfall. Flowering commences approximately 1 year after germination and a fully grown plant can produce 10,000–1,000,000 seeds. The most effective mode of long-distance seed dispersal is through hydrochory (Horton, 1985). This species is found in open and disturbed areas, including wastelands, roadsides and creek lines (Horton, 1985). Cunningham et al. (1981) reported that in Australian arid and semi-arid landscapes, extensive stands of *N. glauca* may persist on stream floodplains and drainage channels after summer floods for some years.

Studies have demonstrated that *N. glauca* is highly toxic to humans (Mizrachi et al., 2000) and other animals (Panter et al., 2000). The species is usually avoided, as it is unpalatable. However, during drought, when food resources are scarce, livestock may consume the plant and die (Cunningham et al., 1981). The plant contains the alkaloid anabasine, which is considerably more toxic than nicotine (Sims et al., 1999). Panter et al. (2000) found that *N. glauca* causes defects in foetal goats and sheep if the mother does not die from consumption of the plant. Furthermore, the presence of *N. glauca* in flooded areas may inhibit the germination of seeds belonging to other species. Florentine and Westbrooke (2005) demonstrated that leachates obtained from dry leaves and twigs of *N. glauca* had a negative impact on the germination of *Lactuca sativa* seeds.

Forward and Robinson (1996) conducted a biological survey of the South Olary Plains, New South Wales, near the South Australian border, which provides the botanical composition and landform data for the South Australian component of the study area. During the survey the authors did not record *N. glauca* in the current study site. A recent study conducted by Florentine and Westbrooke (2005) and Westbrooke et al. (2005) found that *N. glauca* responded to the rare episodic flood event created by high rainfall and invaded the native arid shrubland communities. Florentine and Westbrooke (2005) also reported that larger numbers of *N. glauca* seeds were recovered from the flooded unfenced plot than from the flooded fenced plots, whereas none was found in the (unflooded) control plots. That study found that a large quantity of seed is stored in the soil, although the dynamics and longevity of the small seed is unknown. More importantly, optimal temperature requirements for *N. glauca* seed germination have hitherto been unknown.

Information such as this would be valuable for those devising control strategies for infestations of this species.

The authors also illustrated that the distribution pattern for stem diameter classes of *N. glauca* varied between zones with different flooding histories. Stems measured in the long-term flood zone had an even distribution of height classes. However, in the short-term flood zone, the diameter classes were skewed towards the smaller stem diameter size class. During subsequent months, as flooded areas dried out, *N. glauca* seed deposited in peripheral mud (the short-term flood zone) germinated and formed a dense stand. As Horton (1985) reported, *N. glauca* is a fast growing tree, particularly after substantial rainfall events, and produces flowers approximately 1 year after germination. This species has traits that are comparable with other arid zone weed species (Florentine and Westbrooke, 2005); however, it is essential to understand more about the ecology on this species to enable proper management. In this paper, our objectives were to: (i) examine the population and soil seed bank dynamics of *N. glauca* (ii) compare the germination patterns of *N. glauca* seeds collected from two states in Australia and (iii) demonstrate the effects of flood and drought on *N. glauca* seedlings.

2. Methods

2.1. Study area

The study was conducted on Nagaela Station, south-western New South Wales, around a lake formed in 1997 following a flood of Olary Creek (Fig. 1). For study area details and field experimental design see Westbrooke et al. (2005) and Florentine and Westbrooke (2005).

Detailed vegetation data were collected in September 1999 (3 years and 10 months after the flooding event started), October 2002 (5 years and 10 months after the flooding event started), October 2003 (6 years and 10 months after the flooding event started) and October 2004 (7 years and 10 months after flooding commenced). The data presented here focus on the response of *N. glauca* to the flood event (Fig. 2).

2.2. Investigation of survival patterns of N. glauca in different flood zones

The *N. glauca*-infested area had experienced a dry spell for the past 14 months. *N. glauca* responded to the 1997 rare flooding event, establishing and surviving, but during subsequent years of near average rainfall, *N. glauca* shed leaves and shoot tips dried out.

To examine the survival pattern of the established *N. glauca* plants, we established two belt transects (240 m $\times$ 3 m and 270 m $\times$ 3 m) radiating from the middle of the 'new lake' towards the short-term flood zone. In the long-term flood zone (approximately 1–1.5 m in depth), floodwater stayed for approximately 20 months. In contrast, the short-term flood zone was approximately 30–50 cm in depth and the floodwater remained less than a year, based on the flooding mark. Each transect was divided further into 3 $\times$ 3 m subplots. Within each subplot, we recorded the height (m) and diameter (cm) at 20 cm stem height for all *N. glauca*.

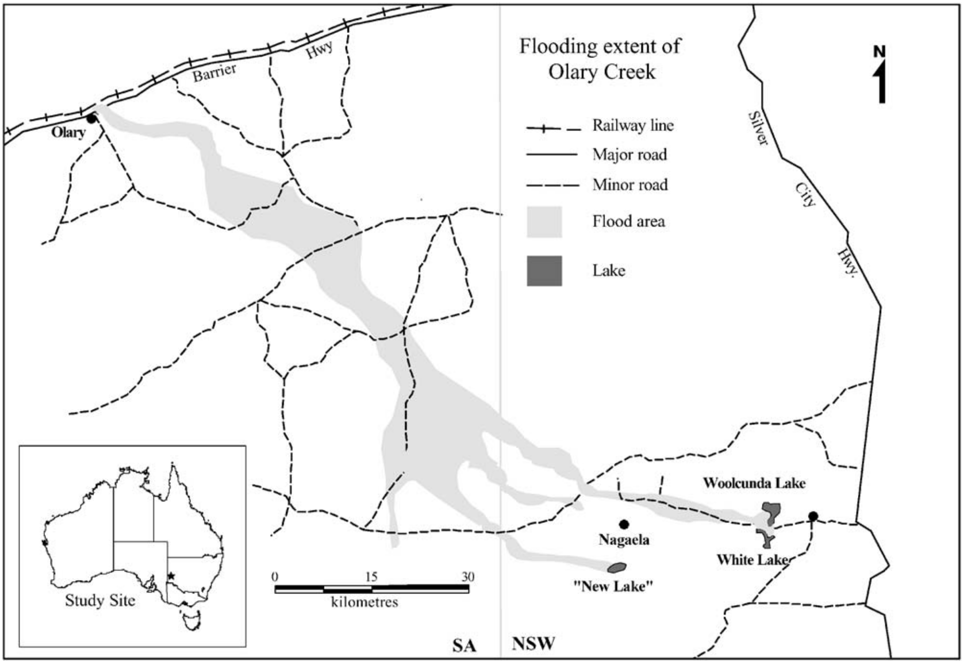

Fig. 1. Location of study site and extent of the 1997 Olary Creek flooding.

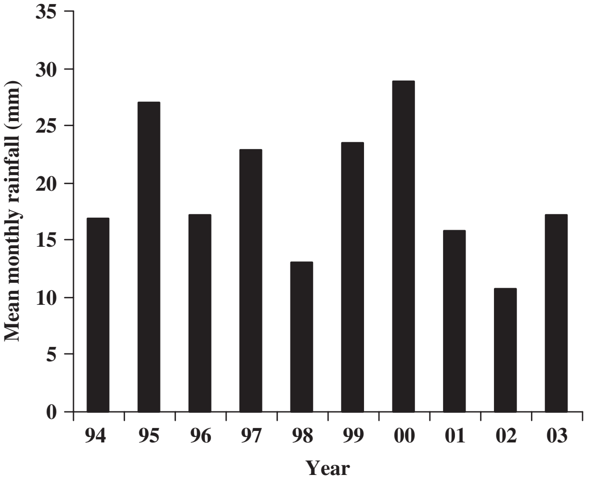

Fig. 2. Mean monthly rainfall (mm) at Tarawi Station, north west of New South Wales from 1994 to 2003.

2.3. *Density of N. glauca seeds in the soil-stored seed bank*

Soil samples were collected from Olary Creek, New South Wales, in October 2003. Twenty samples were taken from randomly selected points (20×20 cm) within each control and exclosure plot. Soil was removed with a small trowel to a depth of 15 cm.

Samples were placed in separate labelled bags, transported to Ballarat and stored in a glasshouse (20–25 °C) for 2 days. Individual samples were thoroughly mixed within the bag to ensure a uniform distribution of seeds and soil, then spread evenly in $28.0 \times 44.0 \times 5.5$ cm trays lined with white Chux® wiping cloth. The trays were placed on benches in a glasshouse. On each bench, a further lined tray containing sterilized soil was placed randomly between the soil/seed sample trays. This was used as a control. All trays were watered for 1 min, twice a day by an automatic mist-spray system. The germinable seed bank was considered as the number of seeds that germinated under favourable water and temperature conditions within 90 days (Bertiller, 1996). This measure provides an estimate of the immediately germinable seed bank. The number of germinated *N. glauca* seedlings was recorded weekly.

2.4. Comparative study of germination patterns of N. glauca seeds collected from new South Wales and South Australia

*N. glauca s*eeds were collected from two populations: Ivanhoe (33° 09′ S; 144° 07′E) in New South Wales and Flinders Ranges (30° 21′ S; 139° 22′ E) in South Australia, during February 2004 and July 2004, respectively. Air-dried but uncleaned seeds were stored in air-tight bottles and kept at room temperature until use. Seeds collected from New South Wales were stored at room temperature for just over 6 months. In contrast, seeds collected in July 2004 from South Australia were kept for less than a month at room temperature. The basal part of the Petri dishes was covered with no. 3 Whatman® filter paper. The filter paper was moistened with distilled water. In each Petri dish, 50 *N. glauca* seeds were placed. Petri dishes were labelled and placed in growth cabinets set at 15, 21, 30, 35 and 40 °C. Each cabinet contained eight Petri dishes, four of which had a 12 h light/12 h dark regime and four of which were in continual darkness (wrapped in aluminium foil). All Petri dishes were kept continuously moist until the experiment was terminated. The seeds were checked every 24 h and any that had germinated were removed from the Petri dish. Seeds were considered germinated when the radicle protruded through the seed coat. The number of seeds germinated, the sum of all germinated seeds and the percentage germinated were recorded daily and calculated. After the initial germinations, any Petri dish that showed no new germinations over three consecutive days was removed and the remaining seeds discarded (Raccuia et al., 2004). All treatments were commenced on the same day and seeds were monitored for 30 days.

2.5. General assumptions

The seed germination study incorporates the following assumptions: Firstly, that seeds collected from New South Wales and South Australia have similar environmental conditions and dormancy conditions; second, that sufficient seed capsules were colleted to cover local variation; and third, that most viable seed collected from South Australia and New South Wales will germinate.

2.6. Flood and drought tolerance

Seeds of *N. glauca* were collected from sites near Nagaela Station (Fig. 1), western New South Wales on 3 February 2004. Uncleaned and air-dried seeds were stored in air-tight bottles and kept at room temperature until use. On 14th February, seeds were sown in sterilized coarse sand in seedling trays. On 15th March, 75 uniform sized (2–3 cm high) seedlings were transplanted into black plastic pots (150 mm high and 80 mm wide) containing a commercial soil potting mixture. Sixty of these were later randomly selected for use in this experiment. All pots were kept in a glasshouse and watered once a day with an automatic sprinkler system. On 6th of April, the seedlings were divided into three groups of 20: control, flooding and drought treatments. Pots were coded with numbered plastic tags. The flooding treatment was commenced by planting five randomly selected seedlings inside each of four plastic tanks filled with tap water. The water level was maintained at 15–20 mm above the soil surface. For the drought treatment, a batch of 20 seedlings was kept separately from flooded and control seedlings. This was mainly to avoid water being splashed on to drought treatment seedling pots. They were initially watered while establishing, but during the experiment, no further water was added. The control seedlings were kept on a table beside the flooding water tanks and watered once a day. The ambient temperature was continually recorded during the experiment. The temperature varied between 19 and 27 °C. All plants were harvested on 25th May, 40 days after the treatments commenced. Each plant was removed from its pot, washed, surface dried between paper towels and placed in separately labelled bags. Plants were then oven-dried at 105 °C for 24 h. Dry weights were obtained separately for shoots and roots.

2.7. Statistical analysis

Seed germination under different temperature and light regimes was analysed using following formula (Saxena et al., 1996)

(1) Final germination (FG) %: the mean percentage of seeds that germinated during the experiment.
(2) Mean period of final germination: $MPFG = \sum N_i D_i / FG$,

where N is the daily increase in seed germination number and D is the number of days after seeds were first placed in the Petri dish.

Mean height growth rate was calculated using the following Relative Growth Rate (RGR) formula:

$$RGR = (\log h_2 - \log h_1)/(t_2 - t_1)\,\mathrm{cm\,cm^{-1}\,week^{-1}},$$

where h_1 is the height (cm) of seedlings when first exposed to the treatments at time t_1, while h_2 is the height of seedlings at the end of the experiment, at time t_2. The time difference is expressed in weeks.

Data were analysed by one-way analysis of variance (ANOVA), using the Super-ANOVA software program (Abacus Concepts, Berkley, CA). Residual plots of each ANOVA were obtained to examine the homogeneity of variance. Based on residual plots, data were transformed to arcsign, log or square root as appropriate and reanalysed. The data presented here are of uniform means. Means were compared using Tukey's HSD comparison (Day and Quinn, 1989).

3. Results

3.1. *N. glauca stem density*

The stem density of *N. glauca* differed between flooded fenced and flooded unfenced plots and varied between sampling times in both the fenced and unfenced plots (Fig. 3). However, the fluctuation pattern was similar, regardless of whether the plots were fenced. A much steeper increase in stem density was recorded between 1999 and 2002 in the unfenced plots than in the fenced plots. In October 2003, the stem density in the fenced plots was 504 compared to 1888 in the unfenced plots. These numbers had decreased to 80 and 432 stems ha^{-1}, respectively, by October 2004 (Fig. 3). At the October 2004 assessment, no *N. glauca* seedlings were found in either the control fenced or the control open plots.

3.2. *Survival patterns of N. glauca shrubs in the different flood zones*

Data presented here are the sum of plants for both transects. The number of plants recorded in both transects was 192. Of those, 52.60% ($n = 139$) were found to have no leaves and to have dried out. Of the 27% ($n = 53$) that survived, 51% and 49% resprouted from the shoot and base, respectively. In contrast, there were only 73 plants recorded in the short-term flood zone, all of which died.

3.3. *Soil seed bank*

The density of *N. glauca* seeds stored in the soil differed significantly ($p = 0.0001$) between flooded fenced (598.75 ± 71) and flooded unfenced (327.5 ± 66) plots. No *N. glauca* seeds were found in the soil collected from the control fenced and control unfenced plots (Fig. 4).

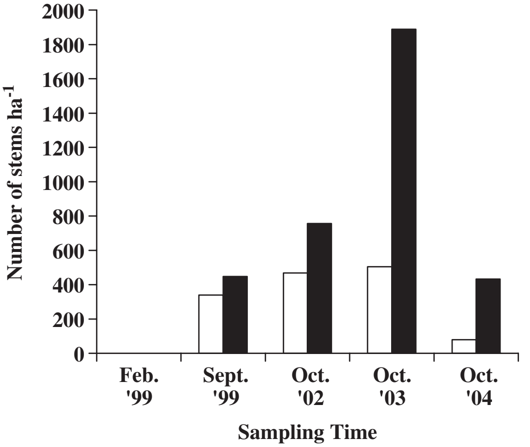

Fig. 3. *N. glauca* stem density recorded in the (□) flooded fenced and (■) flooded unfenced plots at Nagaela Station, north west New South Wales.

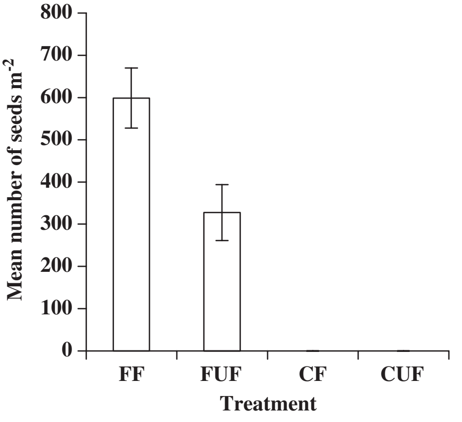

Fig. 4. *N. glauca*: mean number of germinable seeds per square metre in soil samples: FE = Flood fenced (FF), FO = Flood unfenced (FUF); CE = Control fenced (CF) and CO = Control unfenced (CUF).

Table 1
Three way analysis of variance table for the *N. glauca* seed collected from South Australia and New South Wales

Source	*df*	*MS*	*F* value	*p* value
State [S]	1	1170.45	33.94	***
Light [L]	1	594.05	17.22	***
Temperature [T]	4	284.62	824.44	***
S × L	1	26.45	0.7676	NS
S × T	4	117.32	3.40	**
L × T	4	210.92	6.11	***
S × L × T	4	255.32	7.40	***

NS indicates means are not significantly different. Significant differences: at **$p<0.00$; ***$p<0.0001$.

3.4. Germination patterns of N. glauca seeds collected from new South Wales and South Australia

A three-way ANOVA revealed that temperature had a significant effect on *N. glauca* seed germination. Germination rates varied significantly with the main variables (state, length and time) and also with all interactions except state × light ($p = 0.3840$) (Table 1 and Fig. 5).

The mean percentage final germination (MPFG) of the seeds collected from New South Wales increased with increasing temperature when they were kept at a 12 h light:12 h dark ratio. However, the trend was reversed when the dark exposure was increased to 24 h. A similar trend was also observed for the seeds collected from South Australia (Table 2).

3.5. N. glauca seedling response to flood and drought

Before exposure to flood and drought treatment, the seedlings showed no significant difference in initial height ($p = 0.4564$) and number of leaves attached to the stem ($p = 0.4450$). This suggests that there were no substantial associated differences in seedling

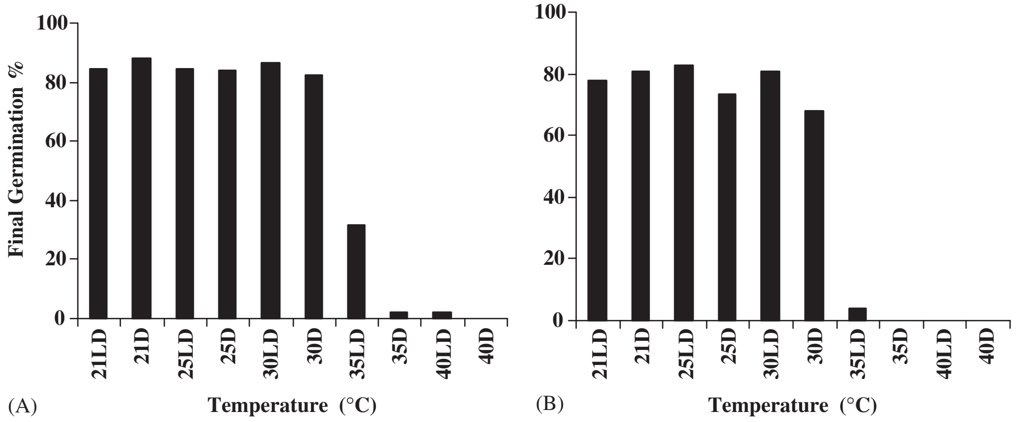

Fig. 5. Final germination percentage of *N. glauca* seeds collected from (A) New South Wales and (B) South Australia when exposed to different temperatures and light regimes. Abbreviations in the '*x*' axis: Initial numerals indicate the temperature (°C) of the environmental cabinet. LD = 12 Light and 12 Dark and L = 24 Dark.

Table 2
Mean period of final germination for *N. glauca* seeds exposed to a range of temperatures

Temperature (°C)	12L:12D		24 Dark	
	SA Mean (se)	NSW Mean (se)	SA Mean (se)	NSW Mean (se)
21	9.94 (0.5)	11.11 (1.73)	12.42 (1.32)	11.30 (0.63)
25	8.22 (0.63)	10.32 (1.25)	10.77 (1.15)	13.90 (0.85)
30	11.84 (1.25)	11.72 (3.40)	10.54 (1.32)	12.85 (1.78)
35	0 (0)	12.20 (1.68)	0 (0)	0 (0)
40	0 (0)	12.25 (3.09)	0 (0)	0 (0)

SA = South Australia; NSW = New South Wales and se = standard error.

morphology prior to treatment. After planting in different treatments, seedling height was significantly ($p<0.0000$) affected in the drought treatment, as were plants in the flood treatment to a lesser extent (Table 3). The final number of leaves attached to the stem, root dry weight, root:shoot ratio and RGR were also significantly affected by drought followed by flood (Table 3). However, no significant differences were found in shoot dry biomass or whole plant dry biomass. Stem hypertrophy (swelling) was observed in waterlogged seedlings. Three weeks after waterlogging, adventitious roots were found to have formed on the submerged portion of the stems and these roots floated just below the water surface. In most waterlogged plants, roots surrounded by soil had become dark, almost black.

4. Discussion

Florentine and Westbrooke (2005) described the initial invasion by *N. glauca* after the 1997 flooding event. In this paper we examine later developments, 7 years after the flooding event. In addition, we examine the density of seeds in the soil seed bank, optimal

Table 3
Mean (±SD) of final height, number of leaves, shoot dry weight, root dry weight, dry weight of whole plant, root:shoot ratio and relative growth rate of *N. glauca* seedlings after 58 days of flooding, and drought

Attribute	Control	Flood	Drought	*F* value	*p* value
Height (cm)	4.42 (0.92)^{a}	2.37 (0.53)^{b}	1.72 (0.17)^{b}	68.56	***
Number of leaves	12.40 (0.94)^{a}	10.50 (2.52)^{b}	9.42 (0.96)^{b}	8.25	***
Shoot dry weight (g)	0.93 (0.48)^{a}	0.89 (0.41)^{a}	0.76(0.18)^{a}	1.11	NS
Root weight (g)	0.68 (0.44)^{ab}	0.45 (0.29)^{b}	0.78 (0.34)^{a}	4.41	*
Whole plant (g)	1.60 (0.75)^{a}	1.34 (0.59)^{a}	1.54 (0.43)^{a}	1.00	NS
Root:shoot ratio	2.21 (2.11)^{ab}	2.80 (2.00)^{a}	1.17 (0.77)^{b}	4.28	*
RGR (cm cm ^{1} week ^{1})	0.57 (0.09)^{a}	0.31 (0.86)^{b}	0.14 (0.19)^{c}	56.07	***

Different letters indicate that means are significantly different (Tukey's HSD test). NS indicates that means are not significantly different. Significant differences: at *$p<0.05$; ***$p<0.0001$.

temperature requirements for germination of *N. glauca* seeds collected from New South Wales and South Australia and the effects of flood and drought on *N. glauca* seedlings. The seed density of *N. glauca* varied significantly over the sampling period. Larger numbers of *N. glauca* seeds were stored in seed banks in the flooded fenced plots than in the flooded unfenced. Light and temperature had no effect on the germination of *N. glauca* seed collected from New South Wales. Flooding and drought had significant impacts on *N. glauca* seedling height, foliage production (number of leaves attached to the plant), root dry biomass, whole plant biomass and also on the RGR. In general, plants exposed to these treatments were shorter and smaller, with less foliage, than control plants (Table 3). In these attributes, the treatments were not statistically distinguishable. However, root mass was significantly greater in drought plants than in flooded plants or controls, even though the RGR of stem was low. This suggests a functional response to water shortage.

Because a high density of *N. glauca* stems was recorded over the period of 5 years, the drastic reduction in *N. glauca* stem density in the study site deserves special attention. Between February 1999 and October 2003 the stem density of *N. glauca* increased exponentially. By October 2003, the density was three times higher than that of previous years (Fig. 3). There are alternative potential explanations for this. Horton (1985) reported that *N. glauca* prefers high soil moisture and this may have provided favourable conditions for seed germination and subsequent establishment by *N. glauca*. As flooded areas dried out, *N. glauca* seed was deposited on peripheral mud, where it germinated and formed a dense stand (Florentine and Westbrooke, 2005). As the newly created lakes dried out during subsequent years, the waterlogged area diminished, progressively creating more suitable surface area. Coupled with suitable temperature and soil moisture, this created ideal conditions for the *N. glauca* seeds to germinate and subsequently establish. If we accept this scenario, it is unclear why the population decreased in 2004. During 2004, the monthly mean rainfall was less than those of the previous 3 years. Lower soil moisture conditions might have reduced seed germination success and/or increased the mortality of germinated seedlings.

The remaining population density of *N. glauca* appears to be declining. Thus, it could be argued that these densities will shrink further in a few years time. Two important conclusions have emerged from this study. Firstly, we found that immediately after sporadic rainfall, 'dead' shrubs were able to produce new shoots, either from the branches or close to root collar. Secondly, the high soil seed bank density suggests that many viable seeds in the soil bank may germinate after rainfall. However, in the absence of data on seed viability, such as how long seeds persist in the soil after their release from the capsule, it is misleading to suggest that seeds from soil bank would continue to germinate after rainfall. However, the resprouting capability after sufficient rain is worthy of mention. Even if the seeds do not persist in the soil for a long period, then the resprouting shrubs should later be able to produce a substantial amount of viable seeds. The seed germination study shows that viable seeds can germinate within 2–3 days after incubation at various temperature and light regimes. Further, the experimental exposure of seedlings to extreme environmental conditions, such as flood and drought, shows that the young seedlings are able to withstand alternating flood and drought events at least for 2 months. Therefore, it is not safe to assume that when the present plant population dies off, there will not be any future *N. glauca* stands. Whatever the case may be, the ecological traits exhibited by this species indicate that extreme care should be taken in the management of elevated populations in arid lands. These traits include high seed production, a substantial soil seed bank, the ability to endure prolonged waterlogged and drought conditions, the capability of resprouting after small amount of rainfall and high seed germination rates over a range of temperatures.

The final germination percentages of New South Wales seeds and South Australia seeds showed significant differences in response to state, light and temperature. There were also significant interactions between state $\times$ temperature, light $\times$ temperature and state $\times$ light $\times$ temperature. Although the seeds were collected from two different populations in two different states, these sites were geographically close to each other (approximately 550 km apart) and shared comparable arid climatic conditions. As Baskin and Baskin (1989, pp. 53–66, 1998) pointed out, seeds of invasive species habitually show seasonal changes in dormancy during dry storage. In addition, the South Australian seeds were exposed to field conditions until mid-winter, whereas the New South Wales seeds were removed from the field in late summer.

Vegetation communities in rangelands experience more or less frequent drought punctuated by infrequent intermittent or episodic flood events. The population dynamics of *N. glauca* shows that mature plants decline and die in the face of prolonged drought. There are at least three important questions to emerge from this. Firstly, is it safe to assume that the current population of *N. glauca* will die off or at least be thinned out as drought continues, eliminating or reducing their ability to recolonize when favourable conditions return? Secondly, if we assume that the area infested with *N. glauca* receives another flood event in the near future, will the surviving plants or seeds in the seed bank be still viable and able to overcome the waterlogged conditions? Finally, are opportunities for the recovery of local populations of *N. glauca* limited to periods of substantial local rainfall? Floods are not necessarily just caused by local rainfall events. Quite distant heavy rainfalls higher in the catchment can also cause flooding and perhaps the dispersal of seeds into the area. Studies by Florentine and Westbrooke (2005) and Westbrooke et al. (2005) showed that *N. glauca* invaded mallee shrubland after a distant high rainfall flood event during the early part of 1997. Further, *N. glauca* prefers sites with high soil moisture for germination and establishment and seedlings exposed to waterlogged condition survived almost 2 months. However, it is not clear to what degree the mature *N. glauca* shrubs will respond to long-term waterlogged conditions. Without a field-based study on how *N. glauca* would respond to prolonged waterlogged conditions we are unable to further discuss this issue. It must be also emphasized that any extrapolation from controlled experiments to field conditions should be done with caution, since a number of biotic and abiotic factors may interact with each other in the field to influence the results.

Zedler and Black (2004) proposed patterns of invasion by *Agrostis avenacea* into new areas. The authors suggested that (i) *A. avenacea* can function as a casual weed in disturbed areas, but (ii) it requires high soil moisture to reach maximum size and achieve seed production, and (iii) it has high seed production and a mode of dispersal that allows it to invade quickly across landscapes. If we compare these three traits with the *N. glauca* invasive pattern, we can say that this species also has the capacity to cross landscapes and to invade and infest areas with high soil moisture. It also shows high seed production. Further, adaptations by *N. glauca* seedlings to extreme weather conditions add one more invasive character to the ecological traits shown by the grass. It appears that *N. glauca* also qualifies as an invasive and resilient weed. As such, it is always safer to take appropriate management action at an early phase of invasion rather than at a late stage in the infestation. To do this, we must first undertake studies such as this to understand the plant's ecological characteristics.

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